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SOME HABITAT RESPONSES OF THE LARGE WATER-STRIDER, GERRIS REMIGIS SAY. III

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VI. Discussion of Experiments at White Heath

1. Rôle Played by Vision.—In regard to the experiments at White Heath there is little to be said more than already has been stated in the discussion in connection with the responses of the water-striders, during severe drought, in the dry bed of the stream. In general, the majority of the gerrids found their way back to the brook, when removed from it to distances of one, two, three, and four yards. This was true whether they faced the brook, were placed with their bodies parallel to its banks, or faced directly away from the water. Water-striders with their heads turned away from the stream took a little longer time to reach the brook than was true of the other hemipterons, and they also evinced more random movements. Occasionally a gerrid wandered astray and seemed unable to reach the brook.

At such short distances away from the water, as have been mentioned, it is very probable that the hemipterons find their way back to it mainly through the sense of sight. It is a well-known fact that many species of aquatic Hemiptera respond positively to light as a stimulus, indicating that vision must play an important part in the behavior of the members of this group. Among these are the water-striders *Gerris orba* (Essenberg, 1915, p. 400), *Gerris remigis*, *Gerris marginatus* (Riley, MS.), and probably *Gerris thoracicus, Gerris tristan* (Kirkaldy, 1899, p. 110). Not only do certain water bugs respond positively to light, but Cole (1907, p. 387) has proved the truly remarkable fact that *Ranatra fusca* possesses the ability to discriminate between two luminous areas of different size, even though they are of the same intensity. Water-striders may possess this sort of discrimination.

At this point I desire to direct attention to certain interesting experiments of Parker (1903) on the butterfly, *Vanessa antiopa* Linnæus, because of their probable bearing on some of the responses of *Gerris remigis.* According to this writer (1903, p. 467),

> *Vanessa antiopa* . . . [is able to] discriminate between light derived from a large luminous area and that from a small one, even when light from these two sources is of equal intensity as it falls on the animal. These butterflies usually fly toward the larger areas of light.

He (1903, p. 465) remarks that in the sunlit spots in the woods, this butterfly responds to the large areas of sunlight rather than to the smaller ones. This form of response applies also to the sun, although

> the retinal image of the sun must be vastly brighter than those of all other spots [of sunlight].

Furthermore, writing of the way in which *Vanessa antiopa* finds a patch of sunlight, he (1903, p. 464) makes the following statement:

> This patch [of sunlight] is found not through the accidental wandering of the butterfly into it, but by the butterfly's taking a direct course to it, precisely as the insect finds a single light window in an otherwise dark room. The directive influence, then, is not the intense sunlight that makes the patch, but the much less intense reflected light radiating from the patch. This must form a localized spot on each retina of the butterfly, and it is the position of these spots that determines the direction of flight.

The surface of the water in a brook forms an excellent reflecting surface, either for moonlight or for sunlight, and it is probable that the gerrids respond to such reflected light much in the same way that they do to artificial light. Or they may respond to water, or rather to the reflections from its surface, according to the same general principle that *Vanessa antiopa* responds to patches of sunlight. These areas of sunlighted water in the brook must have much the same appearance to insects with image-forming eyes, such as water-striders, as do the sunlit areas in the woods. The gerrids go toward the water—not quite so directly as *Vanessa antiopa* moves toward areas of sunlight—with but few preliminary random movements, except in the case of those having their heads directed away from the brook, in much the same fashion and probably for much the same reason that *Vanessa antiopa* goes toward sunlit spots in the woods.

I observed, as early as the summer of 1911, that these water-striders respond to moving objects and shadows more promptly than they do to stationary ones. In the early fall of 1918, I discovered that individuals of *Gerris remigis*, confined in an aquarium, respond definitely and in a pronounced manner to a moving incandescent electric light and also to frequent changes in the position of such a light. Essenberg (1915, p. 402) states that in *Gerris orba*

> The sense of sight is keenly developed, the insects detecting a moving object or a shadow very quickly.

The responses of *Ranatra fusca* to a moving light and also to a light frequently changed as to position are well known through the admirable work of Holmes (1905). He (1907, pp. 160, 161) has also pointed out that the young of *Ranatra quadridentata* respond to changes in position of a light. Therefore, a brook with a current of moderate velocity is more likely to be seen by the gerrids than is still water. The riffles and small waves serve as additional reflecting surfaces for diffuse daylight and sunlight, which facts aid in making the position of the brook still more noticeable to the water-striders.

2. Rôle Played by Moisture.—It is possible that moisture from the brook diffusing through the atmosphere may serve, to a certain extent, as a stimulus which may produce a positive response when the water-striders are in such close proximity to the stream as previously has been indicated. However, I am much in doubt of such an explanation. The plan to prevent the gerrids from seeing the water, or perhaps the reflections from it, and yet not to obstruct the diffusion of moisture from the brook did not produce results sufficiently definite from which to draw conclusions. There is much doubt as to the rôle played by moisture in influencing water-striders to move toward the brook.

VII. Discussion of Experiments at Syracuse

1. *Rôle of Vision.*—The experiments conducted near the large pool in the brook at Syracuse added little information to what has been stated concerning the work near White Heath. I believe that vision was the main factor in assisting the gerrids to reach the large pool of water. There were no obstacles to obstruct the view of the gerrids, the surface of the ground being smooth and flat. The water-striders facing toward the pool and also those having the longitudinal axis of the body parallel with its margin found the water very promptly and with considerable directness, again suggesting the probability that they reached the pool according to the same principle involved in the case of *Vanessa antiopa* in finding the areas of bright sunlight. It must be recalled that the pool of water was, comparatively, of large size and that reflections of light from its surface would be more readily seen than from such a narrow brook as the one near White Heath. It is true that, in the experiments in which the gerrids faced away from the water, there was a little less promptness in reaching the surface of the pool and also some random movements. However, in this series of experiments, also, I believe that the sense of sight was the chief factor involved in assisting the gerrids to reach the water.

In the experiments when forty gerrids were used in each trial, I believe that vision played the chief rôle in directing them to the water, at distances both of one yard and of three yards. It is difficult to see what other factor could have served as a stimulus in assisting the water-striders to reach the pool with such directness and promptness as was displayed.

2. *Rôle of Moisture.*—During all of the experiments performed at Syracuse, it is possible that moisture, evaporating from the pool and diffusing through the atmosphere, served as an additional stimulus in effecting a positive response from the gerrids. Such a possibility is more feasible in this connection than was true in the case at White Heath, for the area of the water surface where the experiments were carried on at Syracuse is very much larger than the area of the water surface at the place in the brook where the experiments were conducted at White Heath.

VIII. SUMMARY AND CONCLUSIONS

This paper treats of certain habitat responses of the large water-strider, *Gerris remigis* Say. The work was done partly near Urbana, Illinois, and partly near Syracuse, New York. Observations were made of the responses of the water-striders trapped in stream pools, during a period of severe drought, for the purpose of discovering what became of them after the pools dried up. These gerrids, being mainly apterous forms, were unable to migrate by flight. Experiments, related to the habitat responses, were performed for the purpose of finding out whether water-striders were able to reach their habitat, a brook of moderate size after having been removed from it and placed on the ground certain distances away.

In the late summer, during a severe drought, with a temperature from 90° to 100° F., water-striders, *Gerris remigis,* frequently were found on stream pools, connected by small riffles, at White Heath, near Urbana. As food became scarce or when a scum formed on the surface of some of the pools, the gerrids migrated, by way of the riffles, to other pools that were free from scum. As the drought progressed, the water-striders were congregated on the few pools that remained. Often the scum, a bacterial growth, killed large numbers of the gerrids.

These stream pools were studied and the responses of the water-striders were observed after the pools dried up.

For an entire day particular attention was directed to one small pool, dimensions 12 × 5 × $\frac{1}{2}$ inches, which became dry at that time. There were twenty gerrids on its surface and they made no attempts to escape, as the pool rapidly became reduced in size.

After the pool had become entirely dry, the water-striders did not move away for a period of ten minutes. The initial locomotor responses were due, primarily, to the drying up of the water. This was the only change in external conditions and there was no other evident stimulus. Similarly, when gerrids were removed from aquaria, where they had been kept in captivity, they became very active when placed upon a solid surface away from the water. This was true even if previously they had been inactive. These water-striders moved with an awkward stumbling gait on land, but they made fairly rapid progress. Their methods of locomotion were by walking and jumping. Not infrequently, when jumping, the gerrids seemed to lose control of the orientation of the body, and sometimes made a turn of 180 degrees.

The gerrids responded readily to contact stimuli, which usually was evinced by them in coming to rest against pieces of dry mud, driftwood, stones, and clumps of dead leaves. They occasionally crawled underneath objects of the character that have been mentioned. They did not remain there permanently, for even after carefully marking the exact place, I never have been able to find them the following day. Shade and a lower temperature, combined with contact, probably were the factors which influenced the water-striders to stay quietly in such places. They did not burrow into the mud, nor into the banks of the brook for the purpose of æstivating until the drought had passed. So far as I was able to observe, the gerrids did not æstivate.

Ten out of the twenty gerrids, or 50 per cent., reached the nearest pool—dimensions 3 yds. × 2 yds. × 5 in.—which was ten yards down the dry bed of the brook away from the site of the former pool where the twenty water-striders were entrapped. The first one to reach the pool did so in 5 minutes and 30 seconds. Another gerrid required fifteen minutes to find the water. The last water-strider to arrive at the pool completed the journey in forty minutes. There was considerable variation as to the time necessary to reach the pool on the part of the others, the average being 14 minutes and 30 seconds.

The direction of locomotion, of the ten water-striders that did not find the pool was mainly up the dry bed of the brook. Four wandered so far upstream that there was little probability of their reaching water. With reference to the six remaining gerrids, two of them jumped into a large crack in the dry mud of the brook channel; two crawled under some driftwood; one worked its way into a clump of dead leaves; and one disappeared while I was observing some other water-striders. The following day I was unable to find any of these gerrids, although I sought for them thoroughly, and had marked carefully the various places where they were seen last on the previous evening.

There was considerable variation, by different individual water-striders, as to the amount of time consumed in traversing the distance between their former abode and the large pool of water downstream. None of the gerrids, that reached the pool, journeyed there along a straight path. Those that were among the first to complete the journey seemed to make the least number of errors in direction. All of them made deviations from the most direct route, and also evinced random movements. They found the pool of water through a blundering method of trial and error. The responses of the gerrids that moved downstream and found the water and also of those that moved upstream and were not so successful were, in the main, very similar, although the latter, traveling a longer distance, made many more erratic movements. In general there appeared to be a lack of definiteness in orientation with reference to the direction of the pool and a lack of promptness in journeying to it.

There appeared to be a tendency on the part of the water-striders to keep moving along the path already taken, unless some other stimulus diverted them. This frequently occurred, and contact proved to be the commonest form of stimulus that brought about such diversion. They wandered along a certain path until some stimulus acted upon them. Then they changed their path and tried another direction. There were times when it was difficult to observe what was the stimulus causing the change in direction. In fact on certain occasions there appeared to be no new external stimulus, no change in the external environment, and yet there occurred a change in direction. Therefore the change in direction probably was due to some disturbance of the physiological condition of the animal brought about by some internal stimulation.

Fifty per cent. of the total number of gerrids entrapped on the surface of the stream pool were successful in reaching water elsewhere. In this instance the water was ten yards away from the site of the pool on which the insects were trapped. So large a number, I am confident, is very unusual, for several other observations of a similar character show that a very much smaller percentage were able to find water after the pools on which they were confined had become dry. In some cases the water was at distances of less than ten yards, while in other cases it was eleven, twelve, and fourteen yards distant. I believe that large numbers of apterous individuals die during periods of long and severe droughts. I have some evidence of this from out-of-door observations. Further, I have found that water-striders, frequently, soon die in the laboratory, when the water in aquaria was permitted to evaporate to dryness. This was true even if the temperature was not higher than 85° F.

Experiments were carried on near Urbana for the purpose of observing with what promptness and directness water-striders, *Gerris remigis,* returned to their habitat after having been removed from it, and also for the purpose of observing their responses while doing so. Twenty water-striders were used at each trial. They were removed quietly from the surface-film and then carefully placed on the ground at distances of one, two, three, and four yards away from the brook. In some experiments the gerrids faced the water, in others they were parallel with the current of the brook, and in still others they faced away from the stream.

In all the experiments in which the gerrids faced the brook, the majority of them regained the surface-film. When they were placed on the ground one yard away from the water, all those that reached the brook did so in less than one minute. In no experiment were there more than two gerrids that did not reach the water. When the water-striders were taken two and three yards away from the stream, they were back again on its surface within 2 minutes and 30 seconds. Those gerrids that were placed on the ground four yards away from the brook displayed more random movements in reaching the water than did those that were nearer to it and a slightly smaller percentage succeeded in finding the brook. Those that reached the water did so within four minutes. The experiments with the gerrids parallel with the brook showed that the majority of them reached the water at distances from one to four yards inclusive. Some individuals required a little longer time to make the journey than did those that faced the brook. Sometimes there was a little delay before they began to jump toward the water. Those that were taken four yards away from the brook evinced more hesitancy and more random movements than was the case with the gerrids placed on the ground at points nearer the water. Experiments with the water-striders facing away from the brook showed again that the majority of the gerrids reached the water from all distances from one to four yards inclusive. There were more random movements and less promptness on the part of the water-striders in these experiments than in any of the previous ones. A slightly smaller percentage reached the water from a distance of four yards than was the case in any of the other experiments.

Experiments were conducted in order to discover whether vision, moisture, or both of these factors functioned as stimuli in influencing the water-striders to find the brook. A barrier was constructed to shut off the view of the stream, but to be so arranged as still to permit moisture to pass through it. However, the barrier proved to be defective in this respect. The water-striders were a little less prompt in reaching the water when the barrier was employed than was the case when it was not used. The information that was obtained regarding the responses of the gerrids proved to be inconclusive. However, I am strongly of the opinion that vision is the important factor in directing these hemipterons to find water.

Experiments, of a character similar to those that previously have been described, were undertaken near a small rapid brook in the vicinity of Syracuse. Near the headwaters was a large pool, its approximate dimensions being 55 × 17 × 2 feet, formed by an artificial dam and on its surface were thousands of gerrids. It was here that the experiments were performed.

The gerrids used in the experiments were taken directly from the surface-film of the pool. Different individuals were employed in each experiment. In all the experiments in which the responses of individuals were recorded, the distance from the pool to which the gerrids were taken was one yard. Six experiments were grouped together for convenience.

In the first, second, and third groups of experiments, the water-striders were placed on the ground facing away from the large pool. In the first group of experiments the total time consumed by all the gerrids in reaching the water was 12 minutes and 14 seconds. The average time required to find the pool was 2 minutes and 2⅓ seconds. In Experiment VII, the gerrid had not yet reached the water after ten minutes had elapsed. Omitting this experiment, the total time necessary for all the water-striders to reach the pool was 2 minutes and 14 seconds, and the average time consumed in finding the water was 26⅘ seconds. In the second group of experiments the total time used by the water-striders to reach the pool was 3 minutes and 6 seconds. The average time required to reach the water was thirty-one seconds. In the third group of experiments the total amount of time that elapsed before all the gerrids had reached the water was 17 minutes and 55 seconds. The average time necessary for individuals to find the pool was 2 minutes and 30 seconds. The gerrid used in Experiment XXVI did not reach the pool and it was observed for 15 minutes and 25 seconds. If this experiment is omitted the total amount of time for all the water-striders to reach the pool was found to be 2 minutes and 30 seconds, while the average time required for the gerrids to find the water was thirty seconds. The results of these experiments are typical of many others. A large majority of the gerrids were successful in reaching the water, only two individuals out of eighteen failing to do so. There were a number of random and trial movements, but in the main, the gerrids returned to the surface-film with considerable promptness.

In the fourth, fifth, and sixth groups of experiments, the initial position of the gerrids was facing the water. With respect to the fourth group of experiments, all the water-striders consumed a total amount of time of 2 minutes and 40 seconds in reaching the surface-film. The average time necessary to return to the water was 26⅔ seconds. The gerrid used in Experiment XXXIV consumed ninety seconds of time before it succeeded in finding the pool. Omitting this experiment the total amount of time required by all the water-striders to return to the brook was 1 minute and 10 seconds, while the average time neecssary to reach the water was fourteen seconds. In the fifth group of experiments, the total amount of time required by all the gerrids to find the pool was 1 minute and 52 seconds, and the average time consumed was $18\frac{2}{3}$ seconds. In considering the sixth group of experiments, it was found that 1 minute and 24 seconds elapsed before all the gerrids were back on the surface-film and that the average time necessary to reach the water was fourteen seconds. The results of these experiments are, in the main, very similar to many others not recorded here. Out of a total of eighteen gerrids not one failed to get back to the water. The water-strider used in Experiment XXXIV was the only one that took an unusual amount of time to reach the pool. On the average, the gerrids used in the second three groups of experiments required, approximately, only about one half the amount of time that was required by the water-striders in the first three groups of experiments in order to reach the pool of water. The gerrids in the second three groups of experiments made fewer mistakes and a less number of random movements in finding the water than was the case in the first three groups of experiments.

Just a brief statement will be made with reference to a series of experiments in which the bodies of the gerrids were placed parallel to the shore of the pool. In other respects the experiments were similar to the groups of experiments, one to six inclusive, the results of which already have been recorded. In general, the results were very much like those obtained in the second group of experiments, with the exception that a little more time was required by the gerrids in reaching the water. There was not quite so much promptness, on the part of the water-striders, in moving toward the pool. They evinced a few more trial directions before arriving at the water and occasionally a gerrid did not succeed in reaching the pool.

A series of experiments was carried out in which the gerrids were not oriented, specifically, with reference to the pool of water. The individual responses were not considered in these experiments, as the water-striders were used in large numbers, but records were made of the number of gerrids that reached the pool and records also were made of the length of time that was necessary to find the water. Forty gerrids were employed in each of the experiments, which well might be considered as mass experiments. They were placed on the ground one yard away from the water in a number of the experiments, and in the case of the other experiments, the water-striders were placed on the ground three yards away from the pool.

The results of the different experiments one yard away from the water were very similar in many instances. Therefore the data will be given of only one experiment. A great majority of the gerrids were back on the surface of the pool within fifteen seconds from the time they were placed on the ground. In thirty-five seconds all but two individuals had reached the water, and in one minute of time all the gerrids were striding back and forth on the surface-film. The water-striders jumped toward the pool with considerable promptness. They made comparatively few errors in direction and few random movements. Sometimes there was a gerrid that did not reach the pool.

In the experiments three yards distant from the pool of water, a great majority of the gerrids were back on the surface-film within forty seconds after they were placed on the ground. In the majority of these experiments, all the water-striders had returned to the water within 2 minutes and 5 seconds. A very few gerrids were not successful in reaching the water. A fair degree of promptness and directness were evinced by the water-striders in jumping toward the pool. There were, perhaps, more errors made in direction of movement than was the case with the gerrids in the experiments one yard away from the water.

In all these experiments conducted at the brook near Syracuse, it seemed probable that the sense of sight was the most important factor in directing the gerrids to the water, although moisture also may have exerted an influence on their responses.

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